Zander, R.H. 2014. Classical determination of monophyly exemplified with *Didymodon* s. lat. (Bryophyta). Part 3 of 3, analysis. Phytoneuron 2014-80: 1–19. Published 6 August 2014. ISSN 2153 733X

CLASSICAL DETERMINATION OF MONOPHYLY, EXEMPLIFIED WITH *DIDYMODON* S. LAT. (BRYOPHYTA). PART 3 OF 3, ANALYSIS

RICHARD H. ZANDER
Missouri Botanical Garden
P.O. Box 299
St. Louis, Missouri 63166
richard.zander@mobot.org

ABSTRACT

The shared ancestral and serial transformative evolutionary relationships of the *Didymodon* s. lat. (Pottiaceae, Bryophyta) group of mosses is investigated. Decibans are used as coarse likelihoods for serial trait transformations in sequential Bayes analysis, here using morphology alone. In convergence analysis, theoretical adaptive radiations and neutral but divergent transformations among the species of the data set are evaluated with estimated deciban support for hypothetical models of serial macroevolutionary change. These are converted to Bayes factors. Direction of macroevolutionary transformation on a caulogram is determined by morphological cladogram position, and maximum Bayes factor (or deciban differential) except when an intermediate taxon may be proposed, either from the extant set or as an unknown shared ancestor that minimizes Bayes factor differences. In cases with model probability near unity, deciban range differences between models are accepted because there was little discrimination with Bayes factors. Estimated monophyly among the segregate genera of *Didymodon* s. lat. is represented by a caulogram of serial macroevolutionary relationships annotated with Bayes factors and deciban differentials for serial species-level transformations.

The moss genus *Didymodon* Hedwig was used (Zander 2013: 80) to demonstrate **superoptimization**, which is the attempted naming of cladogram nodes using novel, advanced trait criteria for determining serial evolutionary transformation direction. The naming of the nodes in that paper was done informally and intuitively in the context of informed expertise, the author having studied the family (Pottiaceae) of *Didymodon* for the past 40 years. Segregate genera were established through cladistic analysis and expert ability to identify **dissilience** (situations of core generative species from which descendants with apparent adaptive or at least novel traits arise). The identification and description of evolutionary process in such dissilient genera is the central means of identifying monophyly for these groups, and this paper sets out what may well be the statistical basis for scientific intuition in classical identification of monophyletic groups.

ANALYSIS OF SEGREGATE GENERA OF *DIDYMODON* THROUGH DECIBAN HEURISTICS

Expert opinion use of decibans is a simple way to use clues in sequential Bayes analysis. Given the assumption that we would like to have a more accurate and reasonable analysis of support than the informal assignment of nearly certain likelihoods as was done by Zander (2013: 80), one can now attempt a formalized heuristic analysis of monophyly in the entire *Didymodon* genus complex consisting of the six segregate genera *Didymodon* s. str., *Exobryum* Zander, *Fuscobryum* Zander, *Geheebia* Schimper, *Trichostomopsis* Cardot, and *Vinealobryum* R.H. Zander. The new method uses sequential Bayes by means of decibans assigned to radiative traits. This formalization is intended to mimic or at least explain the quick apprehension of monophyly of expert scientific intuition. All species weighted for putative ancestral status (i.e., basal species for a monophyletic transformation series) have similar primitive traits for the inclusive s. lat. group. These traits include general and widespread distribution at least relative to the putative descendants, no specialized habitats, moderate size, no specialized or reduced organs, and are sexually reproducing.

Molecular analysis for this group is presently uninformative. A molecular (ITS) analysis of many of the same species of *Didymodon* s. lat. was done by Werner et al. (2005). The results were evolutionarily equivocal as discussed in detail by Zander (2013: 90) because neither heterophyly nor distance on the cladogram beyond that expected from hidden paraphyly or phylogenetic polyphyly were evident.

Does restriction of clues to minimal values degrade analysis? Two different superoptimization analyses are done in each genus' Table, one for assignment of 1 dB (in roman typeface) for each morphological trait, as a benchmark for results from a minimal "clue" to direction of transformation. Then, another assignment is done with variable numbers of decibans (in bold typeface) to reflect estimation of different weights of the clues for each trait (in Italic typeface).

First, any analysis using the present method begins with division of a large group into small working groups of one apparent ancestral species and its evolutionarily derived species, judged by criteria discussed above. Often subgenera and sections indicate such evolutionarily "dissilient" groups. In this case, the infragenera of *Didymodon* s. lat. as promoted to generic status (Zander 2013: 93) were used successfully.

Second, evaluation is done of the chance of species 1 (selected intuitively as ancestral) giving rise to each of the other species as a central hypothesis, assuming groups previously segregated to those with only one extant or postulated generalized ancestral species. The cladogram (Fig. 1) of *Didymodon* s. lat. of Zander (1998, 2013: 80) is used as a preliminary grouping structure for the six segregate genera because it happens to group well the classical subgenera (Fig. 1), which do have only one generalized species. A natural key (e.g., Zander 1993: 82) could just as well be used. These segregates were advanced to genus status by Zander (2013: 93) based on the intuitive assignment of high probability to traits implying directionality of macroevolutionary transformation. Each of these segregate genera is here re-evaluated with sequential Bayes analysis first using a minimal 1 dB for all traits, then second using varying deciban assignments as to probability of macroevolutionary transformation of the specialized species away from each of the most generalized. The deciban assignments are coarse, arbitrarily using only odd numbers, 1, 3, 5 or 7, as approximately as is possible to estimate such assignments. The posterior probabilities associated with multiple decibans can be read off Table 1 in Part 1 of this study.

Third, evaluation is done of the chance of any species n generating species 1 as alternative hypothesis. This is essentially 1 minus the chance that species 1 gave rise to each of the other species. A Bayes factor was calculated from the support values of the central hypothesis and the alternative hypothesis to summarize support for and against the generalized species being the ancestor.

Fourth, when probabilities of descendants that are directly generated by the putative ancestor are each lower than, say, 0.95, the IRCI is figured for the chance that at least one of those species is a descendant. Inasmuch as this is a closed causal group, the fact that one of the direct descendants is reliably a descendant of the ancestral taxon means that they all are. The species with highest probability is then at least tentatively the ancestral species.

Descendants can generate descendants of their own. When there are secondary derivations of two or more species from another descendant species, only those secondarily derived species are used in IRCI calculations. An example is the posterior probabilities of the 1 dB per trait analysis of *Vinealobryum* species. One of the putative descendants, *V. nevadense,* is eliminated as secondarily descended from another descendant. The posterior probabilities of the three putative direct descendants of *V. vineale* are 0.50, 0.61 and 0.61. Combining these through the IRCI formula,

the chance of at least one of the three being a descendant is quite high, 0.93, and thus there is a strong chance they all are. Another example is the 1 dB per trait analysis of *Geheebia* species in which the four apparently direct descendants of the putative ancestral species have posterior probabilities of 0.76, 0.72, 0.67, and 0.76, but an IRCI for these of 0.995, such that one of these taxa are surely a descendant, and thus they all are.

Fifth, with probabilities of two or more models close to unity (100%), Bayes factors are uninformative. Those probabilities near unity, however, are generated by summing evidence in the form of clues. A small difference in probability near unity may provide a low Bayes factor, but may incorporate a major difference in numbers or value of clues. In critical cases, differences in decibans may provide convincing evidence for decisions between hypotheses (models). For instance, in the analysis of *Vinealobryum* (Table 4) with variably assigned dB values, posterior probabilities between the most likely basal generative species 1 (*V. vineale*) and species 2 (*V. brachyphyllum*) are similar for models of each generating direct descendants among the remainder of the species. But adding the decibans for species 1 generating the first tier of descendants, i.e., species 2, 3, and 4, and also for species 2 generating species 1, 3 and 4, the sums of 36 dB and 20 dB reveal nearly twice the evidence or at least significance of the evidence for the first hypothesis, namely 1>immediate descendants (species 2, 3 and 4). The Bayes factor associated with this difference in evidence, however, is only 1.0096.

Clues are external evidence of direction of evolution based on evolutionary theory. In some treatments deciban evidence for the two most likely species (species 1 and 2) is the same, but positive in decibans for species 1 and negative for species 2 (e.g., analysis of *Geheebia* (Table 5). But the values are of different use in that these values do not measure the difference between the two models but between each model and an outside criterion applicable to all the species, a separate model of trait transformation. This is a different use of the same evidential information and the distance in dB as *clues* is thus indeed twice the number of dB involved.

Very high Bayes factors can imply an unknown ancestor. Critical here is the idea that when an ancestral species generates several descendants, any new traits that are shared among such descendants may be considered conservative in that they occur in two or more species or by extension in two or more habitats. This is the case when descendants may be more similar to each other than to the putative ancestor. A shared ancestor may be postulated to encapsulate the conservative traits (see example in *Fuscobryum,* below) and mitigate the high B.F. for such descendants which would otherwise be indicative of membership in a separate genus. So parsimony (as done in cladistics) can be in some cases effective. The traits involved in parsimony must be evaluated first as homologous or evolutionarily connected in some way, however, since traits like isolated distributions and polyploidy (otherwise helpful for determining direction of serial macroevolution) may not be homologously shared.

Conservative traits are easily transmissible. When traits are transmitted from a putative *descendant* to one or more secondary descendants, if such traits are new to the genus, they must then be taken as conservative, that is, they are found in different species and therefore apparently tolerate different selective regimes. If the new traits are multiple, reversals in a *combination* of conservative traits are subject to (low) joint probability of unlinked traits. This must contribute to evaluation of direction of evolution and therefore determination of details of monophyly.

The analyses are presented here in order of numbers of species involved to make understanding the complex analyses easier. Rather than a subset for demonstration purposes, all analyses are given because they each deal with different contingencies:

(1) High B.F. for variable dB assignments but low B.F. for minimal clues (tables 1 and 2).

(2) Postulation of a shared ancestor for descendants more similar to each other than to the progenitor (Table 2).

(3) Derivation of one descendant species from another (tables 3, 4 and 5).

(4) Triple concatenation of descendants supported by no reversals, plus status of a highly derived phenotypically and biotypically diverse descendant with a stenomorphic descendant of its own (Table 5).

Note: Throughout "IDs" means "immediate descendants" of species 1 (i.e., exclusive of secondary speciation of descendant to descendant).

Table 1. Deciban analysis of *Trichostomopsis*. 1 = *Trichostomopsis australasiae*. 2 = *T. umbrosa*. 3 = *T. revoluta*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3
TRAITS	Spec. distrib. human		1, **3**	
	Long whip leaf		1, **5**	
	Bulg. hyal. basal cells		1, **5**	
	Local distr.			1, **3**
	Short leaves			1, **5**
	Unicell. gemmae			1, **7**
	SUM	0, **0**	3, **13**	3, **15**
TOTAL dB DIFF.		1	2	3
	>1		-3, **-13**	-3, **-15**
	>2	3, **13**		0, **-2**
	>3	3, **15**	0, **2**	
POST. PROB.		1	2	3
	>1		0.33, **0.05**	0.33, **0.03**
	>2	0.67, **0.95**		0.50, **0.39**
	>3	0.67, **0.97**	0.50, **0.61**	
BAYES FACTORS		1	2	3
	>1		0.50, **0.05**	0.50, **0.03**
	>2	1.99, **19.95**		1.00, **0.63**
	>3	1.99, **31.62**	1.00, **1.59**	
IRCI TOTAL		0.89, **1.00**	0.67, **0.63**	0.67, **0.41**

Table 2. Deciban analysis of *Fuscobryum*. 1 = *Fuscobryum nigrescens*. 2 = Postulated shared ancestor. 3 = *F. perobtusum*. 4 = *F. subandreaeoides*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3	4
TRAITS	Local distr.			1, **3**	1, **3**
	Lvs. short		1, **1**	1, **1**	1, **1**
	Apex rounded		1, **3**	1, **3**	1, **3**
	Unicell. gemmae			1, **5**	
	Sporoph. lacking			1, **3**	1, **3**
	Leaves dimorphic				1, **7**
	Stems short			1, **5**	
SUM		0, **0**	2, **4**	6, **20**	5, **17**
TOTAL dB DIFF.		1	2	3	4
	>1		-2, **-4**	-6, **-20**	-5, **-17**
	>2	2, **4**		-4, **-16**	-3, **-13**
	>3	6, **20**	4, **16**		1, **3**
	>4	5, **17**	3, **13**	-1, **-3**	
POST. PROB.		1	2	3	4
	>1		0.37, **0.28**	0.20, **0.01**	0.24, **0.02**
	>2	0.61, **0.72**		0.29, **0.02**	0.33, **0.05**
	>3	0.80, **0.99**	0.72, **0.98**		0.56, **0.67**
	>4	0.76, **0.98**	0.67, **0.95**	0.44, **0.33**	
BAYES FACTORS		1	2	3	4
	>1		0.63, **0.40**	0.25, **0.01**	0.32, **0.02**
	>2	1.58, **2.51**		0.40, **0.03**	0.50, **0.05**
	>3	3.98, **100.00**	2.51, **39.81**		1.26, **2.00**
	>4	3.16, **50.12**	2.00, **19.95**	0.79, **0.50**	
IRCI TOTAL		0.98, **1.00**	0.94, **1.00**	0.68, **0.33**	0.78, **0.67**
IRCI 2>3 & 4			0.94, **1.00**		

Table 3. Deciban analysis of *Didymodon*. 1 = *Didymodon acutus*. 2 = *D. icmadophilus*. 3 = *D. rigidulus* s. str. 4 = *D. anserinocapitatus*. 5 = *D. johansenii*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3	4	5
TRAITS	Restricted distrib.				1, **3**	1, **3**
	Epixylic					1, **5**
	High elev.		1, **3**		1, **3**	
	Short basal cells		1, **5**			
	Elong. apex		1, **3**			
	Hygric habitat			1, **5**		
	Asex. gemmae			1, **3**		
	Swan neck lf. apex				1, **7**	
	Sporoph lacking				1, **5**	
	Asex. clavate apical propag.					1, **7**
	Thick, not decid. apex			1, **3**		
	SUM	0, **0**	3, **11**	3, **11**	4, **18**	3, **15**
TOTAL dB DIFF.		1	2	3	4	5
	>1		-3, **-11**	-3, **-11**	-4, **-18**	-3, **-15**
	>2	3, **11**		0, **0**	-1, **-7**	0, **-4**
	>3	3, **11**	0, **11**		-1, **-7**	0, **-4**
	>4	4, **18**	1, **7**	1, **7**		1, **3**
	>5	3, **15**	0, **4**	0, **4**	-1, **-3**	
POST. PROB.		1	2	3	4	5
	>1		0.33, **0.07**	0.33, **0.07**	0.28, **0.02**	0.33, **0.03**
	>2	0.67, **0.93**		0.50, **0.50**	0.44, **0.17**	0.50, **0.28**
	>3	0.67, **0.93**	0.50, **0.50**		0.44, **0.17**	0.50, **0.28**
	>4	0.72, **0.98**	0.56, **0.83**	0.56, **0.83**		0.56, **0.67**
	>5	0.67, **0.97**	0.50, **0.72**	0.50, **0.72**	0.44, **0.33**	
BAYES FACTORS		1	2	3	4	5
	>1		0.50, **0.08**	0.50, **0.08**	0.40, **0.02**	0.50, **0.03**
	>2	2.00, **12.59**		1.00, **1.00**	0.79, **0.20**	1.00, **0.40**
	>3	2.00, **12.59**	1.00, **1.00**		0.79, **0.20**	1.00, **0.40**
	>4	2.51, **63.10**	1.26, **5.01**	1.26, **5.01**		1.26, **2.00**
	>5	2.00, **31.62**	1.00, **2.51**	1.00, **2.51**	0.79, **0.50**	
IRCI TOTAL		0.99, **1.00**	0.93, **0.98**	0.93, **0.98**	0.88, **0.54**	0.93, **0.83**

Table 4. Deciban analysis of *Vinealobryum*. 1 = *Vinealobryum vineale*. 2 = *V. brachyphyllum*. 3 = *V. murrayae*. 4 = *V. nicholsonii*. 5 = *V. nevadensis*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3	4	5
TRAITS	Restricted distrib.			1, **3**	1, **3**	1, **3**
	Bark	1, **1**		1, **5**		
	Short leaves		1, **3**			1, **3**
	Lf. apex decid.			1, **7**		
	Lf. apex cucul.					1, **7**
	Leaves broad above				1, **5**	
	Laminal cells bistrat.	1, **1**			1, **3**	
	Midrib thick					1, **5**
	Lf. marg. revol.					1, **7**
	Repro. by gemmae		1, **3**			1, **3**
	Sporoph. lacking			1, **5**	1, **5**	1, **5**
	SUM	2, **2**	2, **6**	4, **20**	4, **16**	7, **33**
TOTAL dB DIFF.		1	2	3	4	5
	>1		0, **-4**	-2, **-18**	-2, **-14**	-5, **-31**
	>2	0, **4**		-2, **-14**	-2, **-10**	-5, **-27**
	>3	2, **18**	2, **14**		0, **4**	-3, **-13**
	>4	2, **14**	2, **10**	0, **-4**		-3, **-17**
	>5	5, **31**	5, **27**	3, **13**	3, **17**	
POST. PROB.		1	2	3	4	5
	>1		0.50, **0.28**	0.39, **0.28**	0.39, **0.04**	0.24, **0.00**
	>2	0.50, **0.72**		0.39, **0.04**	0.39, **0.09**	0.24, **0.00**
	>3	0.61, **0.98**	0.61, **0.96**		0.50, **0.72**	0.33, **0.05**
	>4	0.61, **0.96**	0.61, **0.91**	0.50, **0.28**		0.33, **0.02**
	>5	0.76, **1.00**	0.76, **1.00**	0.67, **0.95**	0.67, **0.98**	
BAYES FACTORS		1	2	3	4	5
	>1		1.00, **0.40**	0.63, **0.02**	0.63, **0.04**	0.32, **0.00**
	>2	1.00, **2.51**		0.63, **0.04**	0.63, **0.10**	0.32, **0.00**
	>3	1.58, **63.10**	1.58, **25.12**		1.00, **2.51**	0.50, **0.05**
	>4	1.58, **25.12**	1.58, **10.00**	1.00, **0.40**		0.50,.**0.02**
	>5	3.16, **1258.93**	3.16, **501.19**	2.00, **19.95**	2.00, **50.12**	
IRCI TOTAL		0.98, **1.00**	0.98, **1.00**	0.94, **0.97**	0.94, **1.00**	0.74, **0.07**

Table 5. Deciban analysis of *Geheebia*. 1 = *Geheebia fallax*. 2 = *G. ferruginea*. 3 = *G. gigantea*. 4 = *G. maschalogena*. 5 = *G. maxima*. 6 = *G. tophacea*. 7 = *G. leskeoides*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3	4	5	6	7
TRAITS	Moist hab.		1, **3**	1,**3**	1, **3**	1, **3**	1,**3**	1, **3**
	Reddish		1,**1**	1, **1**		1, **1**		
	Lvs. strong rec.		1, **3**					
	Sporoph. rare or lacking		1, **3**	1,**3**				
	Perist. fragile, reduced		1, **1**					
	North distr.			1, **3**		1, **3**		1, **3**
	Pl. very large			1, **3**		1, **3**		
	Lumens angular			1, **7**				
	Lvs. catenul.				1, **5**			
	Asex. gemmae				1, **3**			
	Restr. distr.					1, **3**		1, **3**
	Wet limestone						1, **5**	
	Lf. apex rounded						1, **5**	
	Lvs. ligulate						1, **5**	
	Lf. base decur., not winged						1, **3**	
	Costa subperc.						1, **3**	
	Lvs. whip							1, **5**
	Lf. base winged							1, **7**
	SUM	0, **0**	5, **11**	6, **20**	3, **11**	6, **16**	6, **24**	6, **24**
TOTAL dB DIFF.		1	2	3	4	5	6	7
	>1		-5, **-11**	-6, **-20**	-3, **-11**	-6, **-16**	-6, **-24**	-6, **-24**
	>2	5,**11**		-1, **-9**	2, **0**	-1, **-5**	-1, **-13**	-1, **-13**
	>3	6, **20**	1, **9**		3, **9**	0, **4**	0, **-4**	0, **-4**
	>4	3, **11**	-2, **0**	-3, **-9**		-3, **-5**	-3, **-13**	-3, **-13**
	>5	6, **16**	1, **5**	0, **-4**	3, **4**		0, **-8**	0, **-8**
	>6	6, **24**	1, **13**	0, **4**	3, **13**	0, **8**		0, **0**
	>7	6, **24**	1, **13**	0, **4**	3, **20**	0, **8**	0, **0**	
POST. PROB.		1	2	3	4	5	6	7
	>1		0.24, **0.07**	0.20, **0.01**	0.33, **0.07**	0.20, **0.02**	0.20, **0.00**	0.20, **0.00**
	>2	0.76, **0.93**		0.44, **0.11**	0.61, **0.50**	0.44, **0.24**	0.44, **0.05**	0.44, **0.05**
	>3	0.80, **0.99**	0.56, **0.89**		0.67, **0.89**	0.50, **0.72**	0.50, **0.28**	0.50, **0.28**
	>4	0.67, **0.93**	0.39, **0.50**	0.33, **0.11**		0.33, **0.24**	0.33, **0.05**	0.33, **0.05**
	>5	0.80, **0.98**	0.56, **0.76**	0.50, **0.28**	0.67, **0.76**		0.50, **0.14**	0.50, **0.14**
	>6	0.80, **1.00**	056, **0.95**	0.50, **0.72**	0.67, **0.95**	0.50, **0.86**		0.50, **0.50**
	>7	0.80, **1.00**	0.56, **0.95**	0.50, **0.72**	0.67, **0.99**	0.50, **0.86**	0.50, **0.50**	

BAYES FACTORS	1	2	3	4	5	6	7
>1		0.32, **0.08**	0.25, **0.01**	0.50, **0.08**	0.25, **0.03**	0.25, **0.00**	0.25, **0.00**
>2	3.16, **12.59**		0.79, **0.13**	1.58, **1.00**	1.79, **0.32**	0.79, **0.05**	0.79, **0.05**
>3	3.98, **100.00**	1.26, **7.94**		2.00, **7.94**	1.00, **2.51**	1.00, **0.40**	1.00, **0.40**
>4	2.00, **12.59**	0.63, **1.00**	0.50, **0.13**		0.50, **0.32**	0.50, **0.05**	0.50, **0.05**
>5	3.98, **39.81**	1.26, **3.16**	1.00, **1.40**	2.00, **3.16**		1.00, **0.16**	1.00, **0.16**
>6	3.98, **251.19**	1.26, **19.95**	1.00, **2.51**	2.00, **19.95**	1.00, **6.31**		1.00, **1.00**
>7	3.98, **251.19**	1.26, **19.95**	1.00, **2.51**	2.00, **20.75**	1.00, **6.31**	1.00, **1.00**	
IRCI TOTAL	1.00, **1.00**	0.98, **1.00**	0.97, **0.95**	1.00, **1.00**	0.99, **1.00**	0.97, **0.72**	0.97, **0.72**

RESULTS

Monophyly of *Trichostomopsis* (Table 1)

1. *Trichostomopsis australasiae* (Hook. & Grev.) Rob.: assigned ancestral status with no advanced traits, **0 dB** (0.50).
2. *T. umbrosa* (Müll.Hal.) Rob.: specialized distribution in human environments 3 dB; long, whiplike leaf 5 dB; strongly bulging hyaline basal cells 5 dB; **total 13 dB** (1>2 is 0.95).
3. *T. revoluta* (Card.) R.H. Zander: local distribution 3 dB; short-oval to short-elliptic leaves 5 dB; unicellular gemmae 7 dB; **total 15 dB** (1>3 is 0.97).

Conclusion: Monophyly is supported with Bayes factors for 1>2 of 20, and for 1>3 of 31, well supporting *T. australasiae* as ancestral taxon. See Jeffries (1961) assignments of B.F. significances given above in Table 2 of Part 2. After a separate analysis of only 1 dB per trait (minimal clues to direction of macroevolutionary transformation), the B.F.'s are low and IRCI = 0.89, however, there are several other species in the genus that have advanced traits that would increase this measure.

Species 1 and 2 are the two most likely as ancestral for the group. For dB=1, there is a **difference of 9 dB** between 1>IDs (immediate descendants) (6 dB) and 2>IDs (-3 dB), probability of 1>IDs is 0.799, of 2>IDs is 0.333, B.F. of 2.39. For variably assigned dB, the **difference is 39 dB**, probability of 1>IDs (28 dB) is 0.9984, probability of 2>IDs (-11 dB) is 0.0730, B.F. is 14.

Monophyly of *Fuscobryum* (Table 2)

1. *Fuscobryum nigrescens* (Mitt.) R.H. Zander: assigned ancestral status, **0 dB** (0.50).
2. Postulated shared ancestor of *F. perobtusum* and *F. subandreaeoides*: leaves short-ovate 1 dB; apex broadly rounded 3 dB; **total dB 4** (0.72).
3. *F. perobtusum* (Brotherus) R.H. Zander: local distribution 3 dB; leaves short-ovate 1 dB; apex broadly rounded 3 dB; unicellular gemmae 5 dB; sporophytes lacking 3 dB; stems short 5 dB; **total 20 dB** (0.99).
4. *F. subandreaeoides* (Kindberg) R.H. Zander: local distribution 3 db; leaves short-ovate 1 dB; apex broadly rounded 3 dB; leaves dimorphic 7 db; sporophytes lacking 3 dB; **total 17 dB** (0.98).

Conclusion: The deciban assignments for *Fuscobryum perobtusum* and *F. subandreaeoides* are extreme compared to the 0 dB ground of the putative ancestor *F. nigrescens*. When extreme, membership in a different genus is suggested. The two descendants share two traits, and these can be combined in a presently unknown postulated shared ancestor (species 2 in Table 2). This intermediate taxon lowers the polarization considerably, but if (1) it can be found in nature in the future and has no intermediate other traits, or (2) examination of other species emphasizes clustering of two apparent descendant species, then the causal pool is broken and taxonomic distinction of two

genera is advised. Monophyly of *F. nigrescens* > unknown shared species is supported with a Bayes factor of 2.51, a minor signal that is tolerable because it allows one to reject 1>3 at 100 and 1>4 at 50 and instead countenance 2>3 at 40 and 2>4 at 20. At 1 dB per trait, B.F.'s are minor but for 1>2 and 3 the IRCI = 0.98, while for 2>3 and 4, the IRCI is 0.94, which is just barely acceptable.

Species 1 and 2 are most likely. For dB=1, there is a **difference of 4 dB** between 1>IDs (2 dB) and 2>IDs (-2 dB), probability of 1>IDs is 0.613, of 2>IDs is 0.387, B.F. of 1.58. For variably assigned dB, the **difference is 8 dB**, probability of 1>IDs (4 dB) is 0.720, probability of 2>IDs (-4 dB) is 0.284, B.F. is 2.54, like the IRCI, just barely acceptable.

Monophyly of *Didymodon* s. str. (Table 3)
One might note here that *Didymodon rigidulus* s. lat. in the cladogram of Zander (2013: 80) is presently comprised of *D. acutus* and *D. icmadophilus*.

1. *Didymodon acutus* (Bridel) K. Saito: no advanced traits, **0 dB** (0.50).
2. *D. icmadophilus* (Müll.Hal.) K. Saito: higher elevation habitats 3 dB; short basal cells 5 dB; elongate leaf apex 3 dB; **total 11 dB** (0.93).
3. *D. rigidulus* Hedw.: hygric habitat 5 dB; asexual reproduction by gemmae 3 dB; thickened but not deciduous leaf apex 3 dB; **total 11 dB** (0.91).
4. *D. anserinocapitatus* (X.-j. Li) R.H. Zander: restricted distribution 3 dB; higher elevation habitats 3 dB; unique asexual reproduction by deciduous swan-necked thickened leaf apex 7 dB; sporophytes lacking 5 dB, **total 18 dB** (0.98).
5. *D. johansenii* (Williams) Crum: restricted distribution 3 dB; epixylic substrate 5 dB; asexual reproduction by clavate or cylindric but not swan-necked apical leaf propagulum 7 dB; **total 15 dB** (0.97).

Conclusion: Although the deciban polarization is strong when variably assigned, these species are all clearly related and the differences from the putative progenitor, *Didymodon acutus,* are clearly specializations. Monophyly is well established with Bayes factors for 1>2 of 13, 1>3 of 13, 1>4 of 63, and 1>5 of 32 for *D. acutus* as ancestral taxon. The IRCI figures are high for most transformations but are superfluous because of the high probabilities. If each trait were assigned 1 dB, then B.F.'s are low, but IRCI = 0.99 for 1>rest. For 1 dB assignments, however, IRCI values for certain other species being progenitors are also high, and assigning minimal clue values is not valid for this genus. The decision to derive *D. anserinocapitatus* from *D. icmadophilus* in the caulogram (Fig. 2) is based on a Gestalt evaluation of similarity of habitats and areolation of the excurrent costa.

Species 1 and 2 are most likely. For dB=1, there is a **difference of 12 dB** between 1>IDs (9 dB) and 2>IDs (-3 dB), probability of 1>IDs is 0.888, of 2>IDs is 0.333, B.F. of 2.67. For variably assigned dB, the **difference is 44 dB**, probability of 1>IDs (37 dB) is 0.9998, probability of 2>IDs (-7 dB) is 0.1660, B.F. is 6.02, which is quite acceptable.

Monophyly of *Vinealobryum* (Table 4)
1. *Vinealobryum vineale* (Brid.) R.H. Zander: taken as nearly primitive, some biotypes with two traits shared by some advanced species and assigned a minimal 1 dB each; **total 2 dB**.
2. *V. brachyphyllum* (Sull.) R.H. Zander: short leaves 3 dB; reproduction by gemmae 3 dB; **total 6 dB** (0.80).
3. *V. murrayae* (Otnyukova) R.H. Zander: bark habitat 5 dB; restricted distribution 3 dB; sporophytes lacking 5 dB; odd asexual reproduction 7 db; **total 20 dB** (0.99).
4. *V. nicholsonii* (Culm.) Zander: restricted habitat 3 dB; sporophytes lacking 5 dB; leaves broadened above 5 dB; laminal cells bistratose 3 dB; **total 16 dB** (0.98).

5. *V. nevadense* (R.H. Zander in R.H. Zander, L.R. Stark & Marrs-Smith) R.H. Zander: restricted distribution 3 dB; sporophytes lacking 5 dB; leaves short 3 dB; leaf apex cucullate 7 db; leaf midrib thickened 5 dB; leaf margins loosely revolute 7 dB; asexual reproduction by gemmae 3 dB; **total 33 dB** (0.9995). The reliability of direct transformation with *V. vineale* as basal to the serial clade is apparently near certain (i.e., *V. nevadense* is clearly in this genus), but species 5 is doubtless a descendant of species 2 (highly specialized morphology and habitat, found on margins of range of species 2), from which it differs without trait reversals. Species 2 may be taken as serially intermediate between species 1 and 5.

Conclusion: Sequential Bayes analysis indicates monophyly with *V. vineale* or *V. brachyphyllum* as ancestral taxon of the monophyletic group less species 5 is near certain, with B.F. for 1->3 of 63, and for 1->4 of 25, and for 2->3 of 25 and 2->4 of 10. Given that *V. brachyphyllum* seems specialized for human dispersal, has less biotypic variability, and given that *V. brachyphyllum* shared two advanced traits with *V. nevadense,* then postulating *V. brachyphyllum* as basal progenitor of the genus would require more dB reversals for 2->1 than for 1->2. *Vinealobryum vineale* is the better choice for basal progenitor. If the same were calculated at only 1 dB per trait, IRCI = 0.967. Following the cladogram, acknowledging similarity of the two taxa and contiguity of ranges, and the lack of reversals needed for 2->5, the highly derived *V. nevadense* is considered a descendant of the not-very-advanced species *V. brachyphyllum* by 27 db (0.998+). The IRCI calculation is of no help with this analysis.

Species 1 and 2 are most likely. For dB = 1, there is **no difference of dB** between 1->IDs (4 dB) and 2->IDs (4 dB), probability of 1->IDs is 0.714, of 2->IDs is 0.714, B.F. of 1.00. For variably assigned dB, the **difference is 16 dB**, probability of 1->IDs (36 dB) is 0.9997, probability of 2->IDs (20 dB) is 0.9901, B.F. is 1.0098. For variably assigned dB, there is nearly twice the evidence in favor of 1->IDs than 2->IDs, though B.F. is negligible.

The ancestral taxon of the genus *Vinealobryum,* which is basal toof the whole *Didymodon* s. lat. complex, is presently unclear. Several morphologically complex species in various genera with red KOH reactions are candidates, including *Erythrophyllopsis andina* (Sull.) R.H. Zander, *Mironia stenotheca* (Thér.) R.H. Zander, or perhaps some species of *Bryoerythrophyllum* Chen.

Monophyly of *Geheebia* (Table 5)

1. *Geheebia fallax* (Hedw.) R.H. Zander: assigned ancestral status with no advanced traits, **0 dB** (0.50).
2. *G. ferruginea* (Bescherelle) R.H. Zander: moist habitats 3 dB; plants reddish 1 dB; leaves strongly recurved 3 dB; sporophytes rare 1 dB; peristome fragile, often absent 1 dB; **total 11 dB** (0.89).
3. *G. gigantea* (Funck) Boulay: moist habitats 3 dB; northern distribution 1 dB; plants reddish 1 dB; plants very large 3 dB; laminal cells lumens angular, trigonous 7 bB; **total 20 dB** (0.94).
4. *G. maschalogena* (Renauld & Cardot) R.H. Zander: wet habitat 1 db; leaves catenulate-incurved when dry 5 db; asexual reproduction by gemmae 3 dB; **total 11 dB** (0.89).
5. *Geheebia maxima* (Syed & Crundw.) R.H. Zander: northern areas 3 dB; moist habitats 3 dB; restricted distribution 3 dB; stems and leaves enlarged 3 dB; sporophytes lacking 3 db; **total 16 dB** (0.91).
6. *G. tophacea* (Brid.) R.H. Zander: wet limestone habitat 5 dB; leaf apex often blunt or rounded 5 dB; leaf base often with broad decurrencies but scarcely winged 3 dB; costa often ending before leaf apex 3 dB; peristome reduced 5 dB; **total 24 dB** (0.99).
7. *G. leskeoides* (K. Saito) R.H. Zander: northern areas 3 dB; spray zones, wet areas 3 dB; restricted distribution 3 dB; leaves with whiplike apex 5 dB; leaf base winged 7 dB; sporophytes lacking 3 dB; **total 24 dB** (0.98).

Conclusion: Monophyly of *Geheebia fallax* as basal progenitor is strongly supported with B.F. for 1→all species being higher than 10. *Geheebia maxima* is considered derived from *G. ferruginea* (Fig. 2) as a large, somewhat derived form characteristic of hyperoceanic climates, while *G. gigantea* is apparently an extreme endpoint of the same serial transformation, being even larger than *G. maxima* while *G. maxima* has occasional weak differentiation of the trigonous areolation typical of *G. gigantea*. This triple macroevolutionary transformation series has no reversals. Note here that a B.F. of 1 (as in *G. ferruginea* → *G. maxima*) or indeed any low B.F. is not a negative result, a B.F. of 1 corresponds to a posterior probability of 0.50 for the transformational direction.

Species 1 and 2 are most likely. For dB 1, there is a **difference of 20 dB** between 1→IDs (14 dB) and 2→IDs (-6 dB), probability of 1→IDs is 0.9610, of 2→IDs is 0.2400, B.F. of 4. For variably assigned dB, the **difference is 44 dB**, probability of 1→IDs (46 dB) is 0.999975, probability of 2→IDs (2 dB) is 0.6131, B.F. is 1.63.

Geheebia leskeoides is considered (Fig. 2) derived from *G. tophacea* in spite of the strong deciban polarization of *G. tophacea* because the latter is biotypically rich as well as phenotypically variable, and there are collections that lack many of the derived features of the species. Perhaps it would have been better to select one "most ancestral" of the biotypes of *G. tophacea* for this analysis. The strongly and broadly decurrent leaf margins are shared by both species and exaggerated in *G. leskeoides*. Although Table 5 shows a high B.F. for *G. ferruginea* → both *G. tophacea* and *G. leskeoides*, these last two are considered a different taxonomic set and possibly of an unrecognized genus (distinguished mainly by distinct, broadly decurrent leaf margins or auricles) and the apparent B.F. polarization simply reflects strong differences at a higher taxonomic level. Likewise, the B.F. of 100 for *G. fallax* → *G. gigantea* reflects the high differentiation of the latter species and serves only to emphasize that fact that if *G. gigantea* is a member of the closed causal group, then *G. fallax* is basal to that group if perhaps not the immediate ancestor of all species.

Monophyly of E*xobryum*

Exobryum asperifolium (Mitt.) R.H. Zander is presently the only species in the genus *Exobryum*, yet it has derived traits (for this group of genera) of restricted habitat, brick-red coloration, stem central strand usually absent, and peristome short, erect. Further study may turn up ancestral or quasi-ancestral species in this genus. Until then one must assume that an unknown shared ancestor probably of the genus *Exobryum* connects *E. asperifolium* and *Vinealobryum* or *Geheebia* (see Figs. 1 and 2).

DISCUSSION

Superoptimization confirms the initial cladogram. The intent of formalization is to avoid or preclude psychological bias in heuristics; to demonstrate the utility in interpreting data following established evolutionary theory of classical methods over axiomatic, hyperprecise solely numerical methods; and, discover fundamental aspects of physics and statistics imbued in human scientific pursuits. A re-analysis was done for all segregate genera in the cladogram of Zander (2013) of the genus *Didymodon* s. lat. with individual traits assigned particular deciban measures for probability of transformation from a putative ancestral taxon. This formalization confirmed the general form of the morphological cladogram (Zander 2013) that used the initial intuitive assignment of near certainty to the advanced traits, but details here modified somewhat. That cladogram also was here capable of being compressed into an easily comprehended format, and fits aspects of both cladistic and classical forms of analysis, relying on established evolutionary theory as informative of direction of evolutionary transformation.

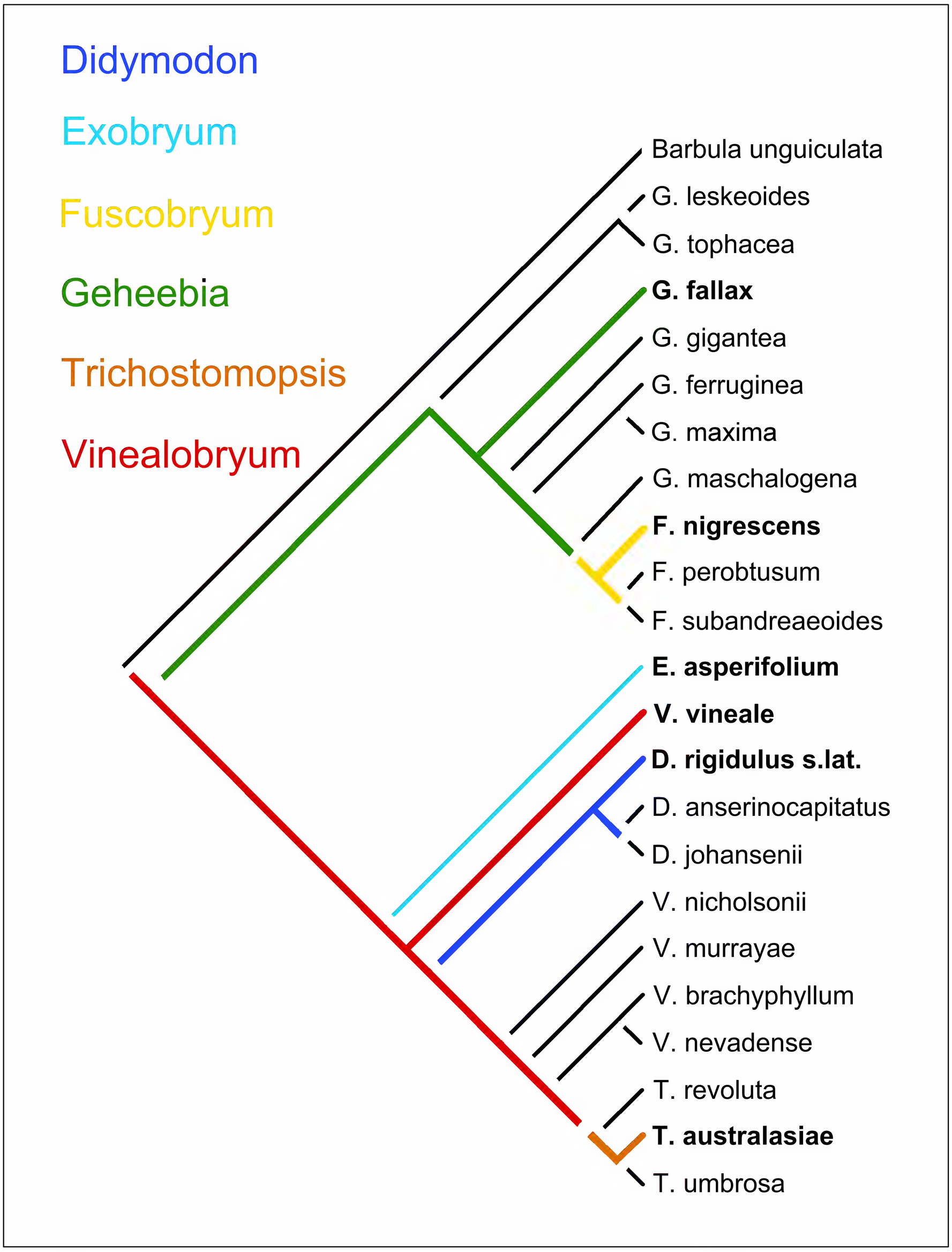

Figure 1. Morphological cladogram of genera in the *Didymodon* s. lat. group, modified from Zander (2013: 80). This demonstration includes only a few of the species known for each genus. Bold colored lines are postulated as deep ancestors of the same name as the generalized species (in bold on the right) and narrower black lines as putative descendants of the generalized species. Decisions for progenitor and descendant status were given intuitively by Zander (2013); formalization of these decisions is given in the tables and summarized in Figure 2.

A caulogram shows both shared ancestral taxa and serial transformations. The caulogram of Figure 2 summarizes the serial macroevolutionary relationships of the *Didymodon* s. lat.

complex estimated from data and theory. Given that software for automatically drawing caulograms does not yet exist, a graphics program must be used. Any software that can make ellipses (see Part 1, Fig. 1) that can be made to touch is acceptable. Or a commagram version (e.g. Fig. 2 of this Part) can be devised by making a circle, erasing a portion, and adding two curving vees. The present author uses NeoPaint (NeoSoft 2012), which is inexpensive but flexible.

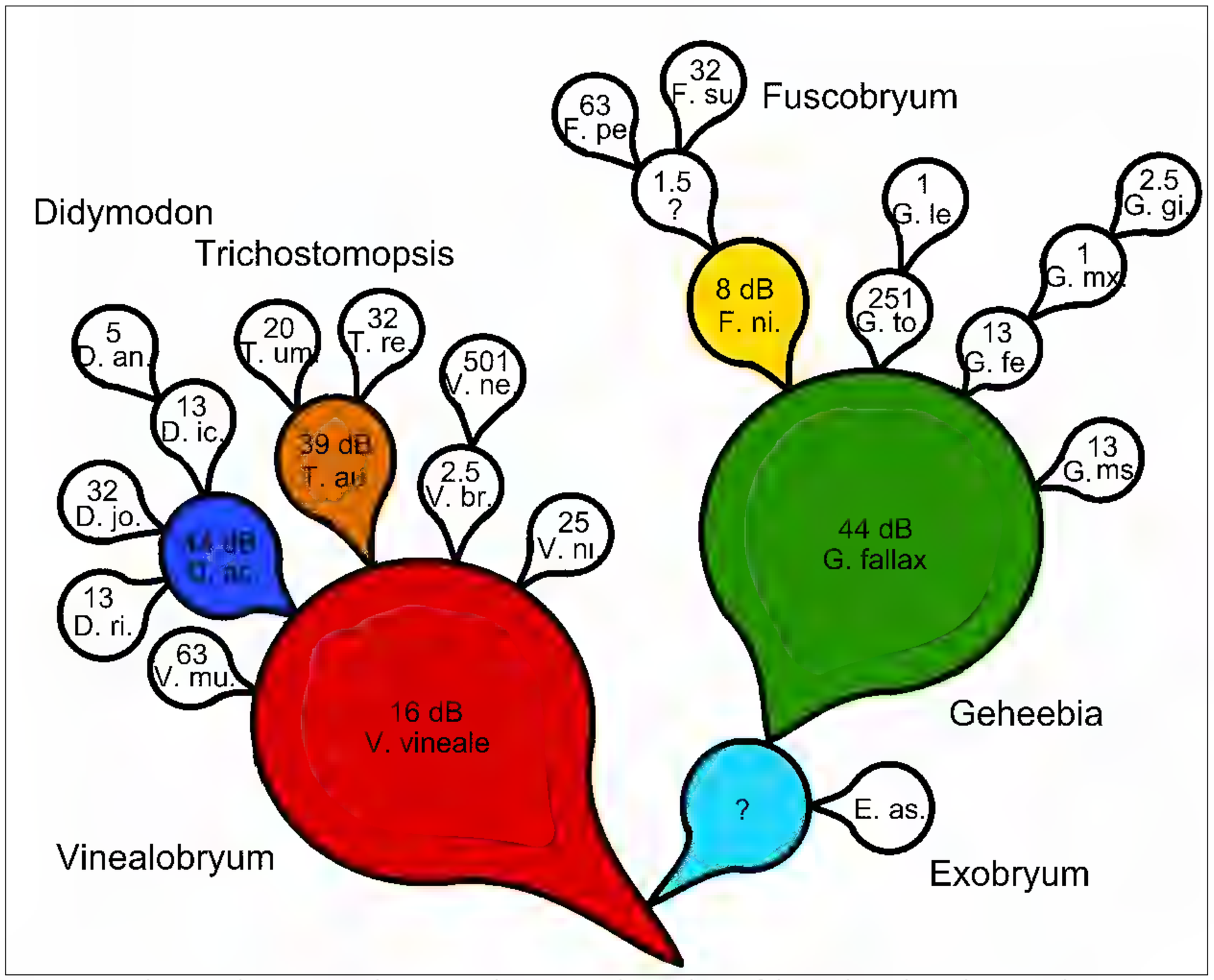

Figure 2 Caulogram showing serial macroevolutionary relationships of the *Didymodon* s lat complex obtained from morphological cladistics and deciban analysis Some species epithets are uniquely identified by two letters Bayes factors supporting direction of macroevolutionary transformation in closed causal groups are given for descendant species based on variable deciban assignments per trait Deciban differences between models of the two most likely progenitors (species 1 → immediate descendants and 2 → immediate descendants) are given for best putative progenitor Question marks denote postulated, presently unknown shared ancestral taxa The macroevolutionary formula (boldface for inferred ancestor) for this caulogram is **vinealis** → mu, ni, (**ac** → jo, ri, (**ic** → an)), (**au** → um, re), (**br** → ne), (**?** → as, (**fallax** → ms, (**to** → le), (**fe** → **mx** → gi), (**ni** → (**?** → pe, su))) Colors denote inferred central ancestral taxa, including the unknown shared ancestor of *Exobryum asperifolium* and *Geheebia fallax,* which is probably a generalist species in the genus *Exobryum*

In Figure 2, Bayes factors are given for each species that is apparently derived from a progenitor, known or unknown, based on transformations of what are taken to be mostly adaptive traits. Deciban differences between models of the two most likely putative progenitors generating the immediate descendants (i.e., exclusive of descendants derived from descendants) are given for the one species most favored as putative progenitor. The probabilities upon which Figure 2 is based are dealt with as clues of various importance, and are frequency estimates only in the sense of informal

expert apprehension of variability during past taxonomic study. Species that are basal and generalist are arranged following cladistic (shared ancestry) relationships using apparently conservative traits. Ability to identify serial relationships and to specify Bayes factors or deciban differences for macroevolutionary transformations is a statistical basis for monophyly. Basing direction of transformation of traits mainly on theoretical adaptive radiations or neutral but unique traits is here substituted for the dubious practice of phylogenetic mapping of trait changes on molecular trees.

No trait reversals is an ideal. The high level of credibility for some polarizations can be overkill for purposes of making a classification, but may be correct given Dollo evaluation of irreversibility of evolution of whole taxa. Both Gould (1970) and Simpson (1953: 311) have pointed out that the chances of the whole genetic system reverting to a complete ancestral state set (as in macroevolutionary reversal to a primitive state set) are infinitesimal. The preferment of no trait reversals in estimating macroevolutionary transformations in the present analysis is important, but may be disregarded in cases of biotypic complexity of the ancestral species (see case of *Geheebia tophacea* above), when no reversals may be expected between a *particular* biotype of primitive traits and a postulated stenomorphic descendant.

Using second-best models is often intuitively clearly wrong. We can say that the chance of one descendant generating another descendant is commonly very small when descendants are more similar to the putative progenitor than to each other. The exception is for situations in which transformation of one descendant into another involves no reversals or for which the reversals are trivial. Radiative adaptation from a generalist ancestor involves or should involve no reversals excepting traits that appear more basal on a standard morphological cladogram than those of the generalist ancestor, and these are commonly few or if many then indicative of higher taxonomic distinction. For example, a putative ancestral-descendant relationship that involves a fully generalized ancestor is supported by positive traits estimated by decibans, and also supported by requirement of no reversal in any advanced traits. But for estimation of the probability of an advanced species actually being ancestor to both the putative ancestor and all the other advanced species, separate reversals from advanced to primitive status are required and very low joint probability comes into play.

At minimum probability levels (i.e., the minimal "clue"), the support via reversal requirement for transformation in the opposite direction is 0.443 probability (i.e., minus one deciban) to the power of the number of (independent) traits requiring reversal. Reversal of four independent (neutral, non-adaptive, or otherwise unlinked) advanced traits at the lowest detectable level of assignable probability (0.433) for each 0.433^4, or 0.035, which translates to a tiny credible interval. But even with a minimal assignment of 0.433 for a set of reversals of a group of linked traits (e.g., all required for adaptation to hygric habitats) when a group of several species involves additional reversals, the additional joint improbability of full and complete reversal of advanced traits in the group if the putative generalized ancestor were *not* the ancestor is decisive. This leads to high Bayes factors comparing odds of a generalized species being basal to the monophyletic group versus that of one of the more advanced species being ancestral, particularly the most advanced species.

There are good heuristics in classical systematics. An appropriate heuristic is when putative descendants are more like the ancestor than each other then they derive directly from that ancestor. Secondary derivation of descendant to descendant is indicated by a no reversal of traits from one descendant to another, e.g., of *V. brachyphyllum* to *V. nevadense*, or of *G. fallax* to *G. ferruginea* to *G. maxima* to *G gigantea*. From the Bayes factor matrices (tables 1 to 5), quite clearly the immediate descendants in general are usually more similar to the immediate progenitor than to each other, except in the cases of apparently secondary speciation either from each other or from a postulated unknown shared ancestral species.

At least in the present case, most nodes can be assigned to known taxa. The object of superoptimization is to parsimoniously determine the minimum of shared ancestors, known or merely inferred, that explain both synapomorphies and autapomorphies. That number of shared ancestors for the *Didymodon* complex of segregate genera is 10 known species, and 2 unknown species (Fig. 2).

CONCLUSIONS

What then is the statistical basis for the heuristic used in classical systematics to estimate monophyly? The Turing decibans are defined as $10^{n/10}$:1. Because they are logarithmic, they can be added. One can easily miss the significance of this when explaining that computers were mere adding machines back in the 1940's. In fact, adding logarithms mentally may be the exact way we use clues every day to make decisions. Things "add up." One clue plus one clue equals two clues logarithmically, five clues plus eight clues equals something more than just 13 clues or probabilistic equivalent of 13 clues, which is a 0.95 probability, the minimum for scientific decisions.

There are 12 inferred ancestral species (Fig. 3) in this study, with 198 total decibans supporting inferred serial macroevolutionary relationships, or 16 dB per taxon transformation. This translates to 0.975 probability or an average of 40:1 in favor of each hypothesis of transformation. This is good evidence that the study was successful.

The details of adding clues involve adding logarithms as with a slide rule. The rapid increase in significance when dealing with clues requires, however, an innate logarithmic scale. Do we have such? Classical systematists certainly do not formally or informally compute $10^{n/10}$:1, or use the complex formula for sequential Bayes analysis. Yet common processes in nature must be described in logarithmic terms. A logarithmic curve is also responsible for a particular sensibility about the use of 0.95 as a basic minimal confidence or credible level for noncritical scientific study, and 0.99 for critical studies. I suggest that deciban-based clues in the context of a mental "slide rule" similar to the logarithmic arrangement of deciban probabilities in Figure 6 of Part 2 of this study may be the way we estimate the serial evolutionary transformation associated with monophyly.

If the average clue is of 5 or 7 decibans, that is, good but not good enough to be convincing about direction of evolution, then this would explain why one character alone is often considered insufficient in classical taxonomy to characterize a new species (13 dB provide 0.95 assurance). This may not be quite as circular as it seems, because it suggests that the perceived value of traits carrying information about direction of serial evolutionary transformation are the unacknowledged criteria for perceived level of species delimitation.

Parallel traits presage conservative tendencies. The cladogram results are accepted here as a quick way of determining direction of evolution of traits that are at least "locally" non-adaptive. This is because a fault of morphological cladograms is used to advantage. A cladogram with genera and species will have species separately derived from the same ancestor randomly associated as sister groups because of parallel traits misinterpreted as those from an unknown shared ancestor. Those "synapomorphic" parallel traits are signals of conservative tendencies presaging evolution of a new genus from the old, and genera distal to such nodes are evolutionarily trailed by one or more nodes in the ancestral genus of ancestral traits implying a transformative relationship at the genus level.

Given uncertainties ignored in phylogenetic analyses, evolutionary caulograms may not be as precise or apparently highly supported as phylogenetic studies. In the case of *Didymodon* s. lat., the segregate genera *Fuscobryum* and *Trichostomopsis* are based on unnamed nodes quite distant from the outgroup in the original cladogram (Fig. 1), an outgroup sufficiently like the above candidates to be acceptable. *Didymodon* is to some extent embedded in *Vinealobryum,* and

Exobryum earns an indeterminate position near the base of the cladogram. The caulogram reflects this. It is possible that analysis of reduction of primitive traits and elaboration by evolutionarily local unique traits through deciban analysis will provide a caulistic substitute, check, or complement to morphological cladistic analysis at the level of higher taxonomic categories, but for the nonce the cladogram of Figure 1 suffices for position of genera in the caulogram.

This paper supports the assertion of Zander (2013: 31) that mathematics, physics, and statistics form the process-based backbone of causal induction of evolutionary relationships involved in classical systematics. This is through formalization of informed, intuitive, Gestalt, or omnispection methods, revealing a fundamental rationale for evolution-oriented taxonomic decisions based on expertise and long familiarity with morphological and ecological variance in groups. Note that advanced traits in *Fuscobryum* were used above to postulate an unknown shared ancestral species intermediate between a putative ancestral generalist taxon and the descendants as a prediction of some future discovery or a retrodiction of an extinct taxon. In this case, the descendants *did not* resemble the ancestor more than they did each other.

Prediction from caulograms means that one expects new or recently studied taxa to either fit into a known serial macroevolutionary transform or to be a generalist ancestor of one or more rather specialized descendants. Cladistics does not and cannot predict in this manner (i.e., what to search for in nature and a process-based explanation for placement in an evolutionary classification). After 250 years of Linnaean taxonomy and 150 years of Darwinian theory in systematics, classical clue-based classification remains highly predictive because well established in both evolutionary and statistical theory.

How we do it. The deciban method of determining monophyly uses both data sets of shared traits (preliminary cladogram) and those of unique or adaptive traits (superoptimization of the cladogram). It is capable of distinguishing serial macroevolutionary changes (rather than branch order excepting parallelism) and can provide a probabilistic basis for evaluation of such changes. The ultimate result is a caulogram (Besseyan cactus) with a Bayes factor assigned to each descendant, or a deciban differential for the first two most likely species when Bayes factors are inconclusive. It is probable that this statistical structure is the long-hidden basis for classical evolutionary systematics.

The future. According to Marois and Ivanoff (2005), the human brain has a hundred billion neurons and several hundred trillion synaptic connections. Humans can decode complex images in 100 milliseconds and store as much as 10^9 bits of information over a lifetime. We are limited by being able to attend to and perform little more than one task at a time. This is due to bottlenecks in information flow, including about 0.5 second for consolidating a stimulus in visual short-term memory, severe limitation in information stored in visual short-term memory, and several hundred milliseconds to select a response. Thus, although our ability to act on information is slow, the flexibility and power of each decision can be immense. This paper gives reasons why computerized analytics based solely on shared ancestry can be misleading, even though fast, precise, and duplicable with different data. A return to human-mediated, thoughtful analysis using classical and certain phylogenetic techniques is not only recommended but is promoted as essential to ensure the effectiveness of evolutionary, biodiversity, and conservation studies.

This paper uses the deciban as minimum clue, about the same as the "just noticeable difference" of a 1–2 percent increase in stimulus intensity in the psychophysics of E.H. Weber (Gregory 1987: 405). Psychophysics is an attempt to formalize and quantify judgment (Poulton 1987: 667). Category rating uses a small range of particular magnitudes that makes judgments easier, such as the 1, 3, 5, and 7 deciban levels used in the present paper. Such ratings provide a logarithmic relationship between stimulus and response:

$$R = K + n \log S \quad (1)$$

where R is the subjective response, S is the stimulus, and K and n are constants.

Information theory (Shannon & Weaver 1963) is presently a well-developed theoretical foundation for cybernetics and data interpretation. Of some relevance to systematic analysis is the fact that data in terms of decibans can be directly converted to data in terms of bits. Decibans and bits both are logarithmic. One ban (10 decibans) corresponds to about 3.32 bits, i.e., logarithm of 2 to the base 10, and a deciban is about 0.33 bits. A 0.99 probability (20 decibans) is about equal to 6.5 bits, while 24 dB yields 0.9962 probability, or 1 byte of 8 bits. Also, 1 standard deviation is 3 dB (or 1 bit), 2 s.d. are 13 dB (or 4.25 bits), and 3 s.d. are 26 dB (or 8.6 bits). Thus, a byte is an unequivocal unit of information (it may be wrong information, but it is decidedly information).

As explained for the non-mathematician by Gleick (2011: 228), the probability of a particular coded message should be a weighted sum of the probabilities of the individual symbols. Log to base 2 (or $\log_2$) is most often used. When the probabilities are equal:

$$H = n \log_2 s \quad (2)$$

where H is the measure of information (or entropy), n is a constant, and s is the number of possible symbols. Note the similarity with the stimulus-response formula (1). Although Shannon entropy equates to uncertainty, this non-intuitive definition can be addressed by interpreting H as how much uncertainty is discarded when the message is decoded. The more uncertainty, then, the better. This is similar to K. Popper's bold hypothesis, which is more meaningful than hypotheses that tell one little when demonstrated correct. When the probabilities of each symbol are different, then:

$$H = -\sum p_i \log_2 p_i \quad (3)$$

that is, information in bits is measured by summing the probabilities of each symbol, p_i, just as decibans are summed in the present paper.

Given similarity of use, equivalencies and dissimilarities of decibans and bits are important. One deciban is the minimum information detectable as a clue, or 0.557 probability. One bit (3 dB) is the minimum information needed to make a decision between two alternatives. That decision is 3 decibans, or 0.666 probability, conveniently 1 standard deviation. A decision at 0.666 probability is only valid in the case of betting on several events, each at 0.666, in which you will come out ahead 2/3 of the time. It is not valid for scientific decisions on which further study is to be based. That high level is 0.95 probability (at least for non-critical decisions), which is 13 decibans or 4.3 bits. This is a little more than half a byte (8 bits), and is the boundary for 2 standard deviations. A byte of information is 24 dB, while 26 dB is 0.997, or 3 standard deviations. This last level of confidence is that for confirmed studies with 0.95 probability.

Given that information theory is highly developed, addressing such subjects as joint entropy, conditional entropy, mutual information, information divergence, source theory, information rate, and other complex techniques for dealing with data, future analysis in systematics (in addition to, say, the Akaike information criterion used in phylogenetics) might well make more use of already well-founded information theory.

SUPPLEMENTARY MATERIAL

Spreadsheets detailing analysis for Tables1–5, calculating Bayes sequential analysis, decibans, and IRCI are available at <http://www.mobot.org/plantscience/resbot/evsy/sprsh>.

ACKNOWLEDGEMENTS

The helpful comments of Guy Nesom are again much appreciated. I thank the Missouri Botanical Garden for superb support and excellent laboratory space over the past 11 years. The users of the listservers Taxacom and Bryonet are as always thanked for fielding my repeated queries and opinions on issues in systematics.

LITERATURE CITED

Gould, S.J. 1970. Dollo on Dollo's Law: irreversibility and the status of evolutionary laws. J. Hist. Biol. 3: 189–212.

Gregory, R.L. (ed.). 1987. The Oxford Companion to the Mind. Oxford Univ. Press, Oxford.

Jeffreys, H. 1961. The Theory of Probability. Third edition. Oxford Univ. Press, Oxford.

Marois, R. and J. Ivanoff. 2005. Capacity limits of information processing in the brain. Trends Cogn. Sci. 9: 296–305.

NeoSoft. 2010. NeoPaint. Ver. 4.7c. Bend, Oregon. <http://www.neosoftware.com>

Poulton, E.C. 1987. Quantifying judgments. In: Gregory, R.L. (ed.). The Oxford Companion to the Mind. Oxford Univ. Press, Oxford.

Shannon, C. and W. Weaver. 1963. The Mathematical Theory of Communication. Univ. of Illinois, Urbana.

Syed, H. and A.C. Crundwell. 1973 [1974]. *Barbula maxima,* nom. nov, an endemic Irish moss. J. Bryology 7: 527–529.

Simpson, G.G. 1953. The Major Features of Evolution. Columbia Univ. Press, New York.

Werner, O., J.A. Jiménez, R.M. Ros, M.J. Cano and J. Guerra. 2005. Preliminary investigation of the systematics of *Didymodon* (Pottiaceae, Musci) based on nrITS sequence data. Syst. Bot. 30: 461–470.

Zander, R.H. 1998. A phylogrammatic evolutionary analysis of the moss genus *Didymodon* in North America North of Mexico. Bull. Buffalo Soc. Nat. Sci. 36: 81–115.

Zander, R.H. 2013. A Framework for Post-Phylogenetic Systematics. Zetetic Publications, St. Louis. CreateSpace Independent Publishing, Amazon.